METSCHNIKOFF ON GERM-LAYERS.[1]

TRANSLATED BY H. V. WILSON.

SOME of the most fundamental principles of the comparative embryology of to-day can be traced back, with a greater or less change of form, to the beginning of the century. Among such is the idea embodied in the following law, which was enunciated by the school of natural philosophers in Germany: "The evolution undergone by every animal from the beginning of its life corresponds to the evolution which is to be observed in the series of animals." The law as thus stated met with opposition from Von Baer (1),[2] who maintained that the embryonic stages of an animal are by no means to be compared with other adult forms, but with the embryos of these forms. He had finally to admit, however, that the difference between these two views is not nearly so great as it appears to be at first sight.

Already animated by this philosophical generalization, embryology received a great stimulus from the parallel Louis Agassiz drew between the embryonic stages of existing animals and the main stages in the geological development of the animal kingdom. Agassiz himself failed to make the right deductions from this truth.

While students of embryology were thus engaged in looking for general points of similarity, on the one hand, between embryonic stages of animals and existing adult forms, and between embryos and extinct animals on the other, Huxley, in 1849, instituted the comparison between the germinal layers of Vertebrates and the layers of the Cœlenterate type. To the latter he gave the names of ectoderm and endoderm. This idea did not remain unnoticed in England, but was generalized and given a popular character by Herbert Spencer in one of his beautiful essays, entitled "The Social Organism." Let me quote from the English philosopher: "Throughout the whole animal kingdom, from the Cœlenterata upward, the first stage of evolution is the same. Equally in the germ of a polype and in the human ovum, the aggregated mass of cells out of which the creature is to

[1] The following paper forms the closing chapter of Professor Elias Metschnikoff's "Embryologische Studien an Medusen," Wien, 1886.

[2] The numbers in this article refer to the bibliographical list appended.

arise, gives origin to a peripheral layer of cells, slightly differing from the rest which they include; and this layer subsequently divides into two,—the inner, lying in contact with the included yelk, being called the mucous layer, and the outer, exposed to surrounding agencies, being called the serous layer: or, in the terms used by Professor Huxley in describing the development of the Hydrozoa, the endoderm and ectoderm. This primary division marks out a fundamental contrast of parts in the future organism." The share each layer takes in building up the developing animal is then touched upon, after which the author proceeds to draw an analogy between the layers of an animal body and the grades of society, in which he compares the ectoderm with the higher grades, the endoderm with the lower grades, and the mesoderm with *tiers-état.*

Huxley's theory for a long time found no supporters in Germany. In that country there was noticeable a certain reaction against the general application of the doctrine of the germinal layers. This reaction reached its greatest height in the well-known paper by Weismann on the embryology of the Diptera. Such a tendency was in perfect accord with the doctrine of types then prevalent, according to which morphological comparisons could only be made within the limits of one and the same great group.

The similarities in the structure and development of animals were long regarded as the expression of a universal plan, which was of a purely ideal nature. In the last two decades it has been generally recognized that at the bottom of these similarities lies genetic relationship. The value of embryology as a key to this relationship was recognized by Darwin, who laid special emphasis on the view that the embryo, being less differentiated than the adult, ought to afford us valuable information concerning the structure of its ancestors; and that when the embryos of two animals are alike, the similarity is due to a common descent. He attempted to illustrate these general laws by concrete examples, and where he met exceptions, he explained them by supposing the embryonic record to be obscured by larval adaptations and precocious inheritance. Darwin thus came to the conclusion that the parallel Agassiz had pointed out is due to the blood relationship of animals, and that this parallel is thoroughly revealed only in cases where the process of develop-

ment has not been altered by the introduction of any obscuring disturbance.

The embryological principles of Darwin were developed in a deductive manner by Fritz Müller in his important little book, "Für Darwin," and were illustrated by many facts chosen from the life histories of the lower animals. The way Müller looked at his facts revealed the manner in which the problems of comparative embryology must be approached in future. He especially emphasized his belief that individual development only repeats genealogical development in cases where the descendants (in the course of their embryology) travel without swerving the straight path which leads up to their ancestral form, "where, however, they do not stop, but press farther on." "In the short space of a few weeks or months," says Müller, "the ever-altering forms of the embryos and larvæ present to our eyes a more or less perfect picture of the changes through which, in the course of countless ages, the species has struggled up to its present condition." In connection with Darwin's ideas on the disturbance of the developmental process, Müller formulated this proposition: "The historical record preserved in the development of the individual is gradually lost, since there is always at work a tendency to make the path from the egg to the adult as straight as possible. The record is, moreover, falsified because of the struggle for existence in which the larvæ that lead an independent life have to take part."

This book of Müller's marked an epoch; and in part under its influence there was soon begun a very active overhauling of the facts of animal embryology, in which more attention was paid to the lower animals than to the higher Vertebrates. Independently of this movement, Kölliker, in 1865 (in the second part of his "Icones Histologicæ," p. 90), came to certain general conclusions, which essentially coincided with the views of Huxley. "Whatever the cause may be," says Kölliker, "the uniformity in structure of a Hydrozoan and a young Vertebrate embryo is a very striking fact; and if this question is pursued further with an eye to the structure and histological development of many animals, it is pretty certain that some simple law of development will be discovered. The problem was before long a subject of busy investigation. The forsaken theory of the germinal layers was again taken up in the realm of the Invertebrates,

and was enriched with many fresh facts, so that it soon became the password to the new road upon which embryology had entered. The theory received the greatest impulse from Kowalevsky's discovery of the development of Amphioxus (2). The embryology of this animal disclosed phenomena which linked together the development of Vertebrates and Invertebrates. As soon as Kowalevsky had discovered the two-layered ciliated larva of Amphioxus he began to look for analogous embryonic forms in other animals, and succeeded in establishing a great number of very valuable facts. These investigations, having for their object the discovery of the most fundamental embryonic forms, such as might be compared with the early stages of Amphioxus, were naturally followed out on animals of low grade with simply organized larvæ. On the other hand, I turned my attention to the development of the higher Invertebrates, with the design of establishing here also the germ-layer theory. I first studied the embryology of Sepiola (4), found two germinal layers, and observed the part each played in building up the organism. Following up the investigation in the group of Arthropods, I failed to demonstrate satisfactorily the germinal layers in Insects, but found them in the higher Crustacea (5) (Nebalia), and particularly well in the scorpion (6). In the latter animal I at first (1866) found only two layers, but soon after (1868) discovered the third. I showed in the scorpion that the upper layer gives rise to the central nervous system; that the middle splits into two layers and forms a series of hollow segments, by the fusion of which the body cavity arises; and that, finally, the under layer becomes the lining membrane of the alimentary canal. Supported by these facts, I concluded, in 1869 (in a publication of the Educational Bureau), that the three layers of the scorpion embryo corresponded in all respects to the three Vertebrate layers. I was not deterred from this view by my belief at the time that the nerve-fibres were derived from the middle instead of the upper layer, since the peripheral nervous system of the Vertebrates was then generally considered to be mesoblastic. Thus the problems of comparative embryology were attacked on two sides, with the object of getting a good basis of facts. It was not until I had made out the main features in the formation of the germinal layers of the scorpion that Kowalevsky began to investigate the embryology of the Oligo-

chæta and Insecta (3). He found in these animals the same three layers, and carefully studied their changes. The rejuvenated germinal-layer theory had now gained a firm basis in the domain of the Invertebrates, and comparative embryology took a new direction, mainly under the guidance of German and Russian investigators. Since the idea of the germinal layers was taken from the higher animals, and was then applied to the Invertebrates, it was natural that misconceptions should arise, owing to such an anti-genealogical method. Some of these misconceptions have lasted until to-day; for instance, in cases where the determination of the several layers is beset with doubt there is often too much stress laid upon purely topographical characteristics. The Orthonectidæ and Dicyemidæ afford two such cases. In these animals certain cells, whose function is generative, are styled endoderm, merely because they lie beneath the external layer. Ed. van Beneden (14, 15) goes so far as to consider the topographical position as the one guide in determining the germinal layers. To quote his own words: "We designate as endoderm the layer or mass of cells which is enclosed, whatever be the tissues derived from it." Haeckel must in this respect be accredited with having made an important step forwards, when he sharply formulated the view, according to which the germinal layers, or at least the two chief layers, are to be regarded as primitive organs (16). From this stand-point a structure in question could only be called endoderm when it possessed several characteristics of this primitive organ, and not when it merely agreed with the organ in topographical position. If, for example, the enclosed mass of cells in the Orthonectidæ were digestive in function there would be no doubt that they represented an endoderm; but since the cells in question are sexual cells, there is very considerable doubt. The main difficulty in the determination of the layers is due to the fact that the genealogy of the germinal layers does not rest on a safe basis, since we know nothing of the primitive condition of the Metazoa. To get an idea of their original condition one must frame hypotheses, such as coincide with as many facts as possible. From a mere hypothesis the doctrine of descent grew to a stable theory as soon as it was shown what a number of phenomena were explicable with its aid and that no fact contradicted it. In like manner hypotheses, which seek to elucidate the original condition

of the above-mentioned primitive organs, should only be given the rank of theories when they are in harmony with our actual knowledge.

The transitional stages between the Protozoa and Metazoa do not appear to exist at the present day. Endeavors have been made, however, to fill this gap in our knowledge by means of hypothetical organisms. There are two ways possible for such a transition to take place,—either by a differentiation of protoplasm around the separate nuclei of a multinucleate protozoan, or by the union of the several individuals of a protozoan colony into a many-celled individual. We will discuss the former method of transition first, and then take up the latter. A close relationship was some time ago supposed to exist between the ciliate Protozoa on the one hand, and the Turbellarians on the other, especially the larvæ of the latter. On the supposed kinship between the two groups there have been built up hypotheses relating to the descent of the Metazoa. Such hypotheses have as their kernel the transition of multinucleate Protozoa into Metazoa, and have been adopted by several investigators, among whom we must mention Jehring (19) and Saville Kent (20). From the stand-point here taken, the mouth and anus of the Infusoria are homologous with the like organs in the Metazoa. Indeed, Jehring believes that the water vascular system of the latter has been derived from the contractile vesicle of the Protozoa. Looking over the whole field of embryology, we find the formation of the blastoderm in Insecta to be the process most in accord with this hypothesis. It is, in fact, on the first stages in the development of the Aphides that Kent mainly rests his belief. Considerations of this kind clearly show that such a hypothesis cannot be maintained. While ignoring all the embryological facts of the lowest Metazoa, the theory harmonizes with the formation of the blastoderm in the Insecta; that is, in a group which has suffered in every respect great secondary changes. But even in this group there are forms that contradict the hypothesis, as, for example, the Poduridæ, insects which in other respects occupy the lowest position in the class, and agree in the segmentation of the egg with Myriapods. When the facts are these, no value can be ascribed to the homologies drawn between the mouth, anus, and water vascular system of the Infusoria and Metazoa.

On the other hand, the hypothesis which supposes that colo-

nies of flagellate Infusoria were transformed into primitive Metazoa explains very clearly the most important phenomena of metazoan development. On this view the segmentation of the egg, and especially the more primitive total segmentation, has been derived from the division which the Flagellata undergoes in building up a colony. In like manner the fact that the cells of so many blastospheres are ciliated is probably due to inheritance from the Flagellata. This hypothesis forbids our homologizing the mouth and other "organs" of the Protozoa with the like parts of the Metazoa, but on the other hand enables us, as Bütschli (21) first pointed out, to comprehend the origin of sexual multiplication. As a fact most embryologists, Ray Lankester and Balfour among others, have adopted this second hypothesis, and after a prolonged trial it has become a basis for further speculations.

Having progressed this far, we should ask ourselves whether it is not possible, with the help of our present knowledge, to determine more or less exactly the nature of those Flagellate colonies from which the Metazoa are descended. Bütschli (22) believes the Metazoa have had a double origin,—the Sponges he derives from colonies of the Choano-Flagellata, the rest of the Metazoa from colonies of true Flagellata. Aside from the fact that there is very little ground for such a venturesome assumption, we must remember that the two groups (of Flagellata) are not sharply separated, and that the collar, which constitutes the main point of difference, is in some cases entirely retracted. As to the relationship of the Sponges to the Cœlenterates, I shall have a word to say farther on.

Whether the Flagellata from which the Metazoa are descended had a collar or not, they were certainly able to take in solid bits of food. This is to be inferred from the great prevalence of intracellular digestion among the lower Metazoa. Taking into account this characteristic of the Metazoa-Flagellata, I cannot believe with Bütschli that the process of nutrition is not worth considering in connection with the question of the metazoan descent. Bütschli is of this mind "because the physiology of nutrition varies exceedingly in the group of Flagellata, without regard to the morphology" ("Remarks on the Gastræa Theory," p. 417). I believe, on the contrary, that the further differentiations undergone by the ancestral colonies were by no means

independent of the method of nutrition. While in some colonies vegetable pigments were found to assist the process of assimilation, others, retaining the method of animal nutrition, gave rise to individuals whose special function it was to seize and digest food. That this conclusion is not purely deductive is gathered from a comparison of such Flagellate colonies as the Volvocineæ and Protospongia.

It would be much to the interest of further deductions if we possessed some actual knowledge of the development of these hypothetical colonies. That they must have been propagated sexually is clear from the multiplication of Volvox. Indeed, the existence of sexual multiplication is a strong argument in favor of the descent of the Metazoa from the Flagellata. As regards a sexual multiplication, the existing Flagellata divide and exhibit some variety in their division. The true Flagellata divide for the most part longitudinally, but transverse division occurs in some species, for example in *Phalansterium consociatum* according to Cienkowsky (24), and in *Ph. digitatum* according to Stein (25). In the Choano-Flagellata, also, both kinds of division have been observed, even in closely-related forms. Thus, according to Kent, *Salpingœca campanula* suffers longitudinal division (20), while all the other species of this genus divide transversely. "The simultaneous occurrence of longitudinal and transverse division in one and the same form has, however, been hitherto established only for certain Chlamydomonadinæ (23). Since in animals that build up colonies the division of the individual plays an important part in determining the shape of the stock, it is important to learn how the hypothetical Metazoa-Flagellata behaved in this respect. Let us recall the generalization made in the second chapter, that the first three planes of segmentation lie in the three dimensions of space. We found this to be true for Medusæ that suffer totally different developments (for hypogenetic as well as metagenetic Medusæ, and regardless of the various ways of forming the endoderm, etc.); and it holds for animals in general, however different they may be, that undergo total segmentation. We are therefore justified in assuming that the same kind of division prevailed among the ancestors of the Metazoa. There is the more reason for this assumption in view of the many ways in which it is possible for an embryo to be built up, of which an idea may be obtained from plants and ani-

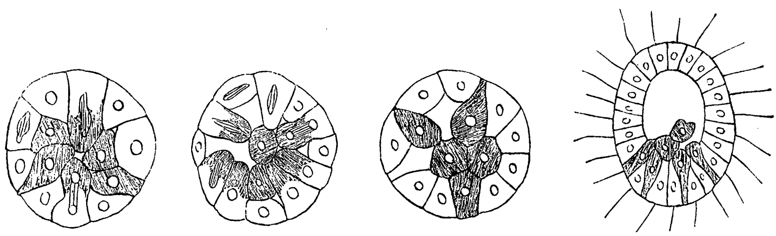
mals with unequal segmentation. Even the formation of a blastosphere can take place without the occurrence of the typical first three divisions. Thus, in Volvox, all the divisions are meridional, the result being a plate-like embryo resembling Gonium. There is no segmentation cavity, and the blastocœle is formed by the gradual growth of the plate towards one pole (22, 23, 25). If we are to use the process of segmentation at all for genealogical purposes, the assumption adopted above seems inevitable. It is, moreover, not without the support of analogous cases in the organic world, as is learned from the divisions undergone by the Schizomycetes. Most of these forms divide transversely, but there are a few exceptions with longitudinal division, for example, a peculiarly branched species parasitic in *Daphnia pulex*, discovered and described by me as *Dendrobacterium oculatum*. Besides such bacteria where there is but one kind of division, there are others where the cells divide in two meridional planes, as in the micrococci of gonorrhœa; and yet others like Sarcina, where the divisions follow the three dimensions of space and consequently agree with the total segmentation of most Metazoa, and also with the assumed division of the hypothetical Metazoa-Flagellata. Since in the typical cases of total segmentation the segmentation cavity appears after the third division, and the embryo is very early transformed into a blastosphere, it is probable that the ancestors of the Metazoa swam about as blastosphere-like colonies.

If we accept these peculiarities of the Metazoa-Flagellata as a basis for further speculations, we are enabled, it appears to me, to throw a certain light on the origin of the primitive organs. Embryology teaches us that the endoderm is formed in very different ways among the Medusæ. In recapitulating these various methods, I have first to state that the endoderm arises either at several points of the embryo or only at one point. In the first case the origin is multipolar, in the second unipolar (in the latter the pole is always at the hinder end of the larva). The multipolar type of formation appears either (*a*) as a multipolar immigration of the cells from the surface of the blastosphere into the interior; (*b*) as a primary delamination by means of the transverse division of the cells of a blastosphere; (*c*) as a secondary delamination following upon the formation of a morula; or (*d*) as a mixed delamination, where the endoderm is in part

formed by transverse division and in part by immigration. These methods of forming the endoderm are not all sharply separated; on the contrary, transitions exist between some of them. The unipolar type appears either (*a*) as an immigration of the blastula (or blastosphere) cells from the hinder end of the larva, or (*b*) as an invagination.[1]

The question is now, What is the stand-point from which a comprehensive and intelligible view may be got of these various methods of forming the endoderm, and which of the existing theories on the origin of the primitive organs is best able to explain the facts? It is at once seen that on assuming the descent of the Metazoa from multinucleate Protozoa (Infusoria, or perhaps Heliozoa and Radiolaria), we become entirely unable to explain either immigration from the surface, or primary delamination, or invagination. It is unnecessary for me to go into a detailed criti-

[1] Multipolar immigration is illustrated by Fig. 3. From various points of the blastula cells migrate into the interior; and, their number increasing, they here form a solid mass of endoderm, which is subsequently hollowed out to form the digestive cavity. This method occurs in Æginopsis (Atlas to the original paper, Plate IX.). Fig. 2 illustrates primary delamination, found in the Geryonidæ (Atlas, Plates V. and VI.). The inner ends of the blastula cells are constricted off to form the endoderm. They very soon arrange themselves in the shape of a hollow sphere, the cavity of which becomes the permanent digestive cavity. Secondary delamination is the rule



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among Hydroids without a free medusa stage. It is essentially like mixed delamination, Fig. 1, but differs from it in the very late appearance of any histological difference between the superficial layer of cells and the included or endoderm cells. Neither in this type nor in mixed delamination is there an obvious blastosphere, the cell immigration and transverse division commencing at a very early date. In both types the solid endoderm is subsequently hollowed out to form the digestive cavity. Mixed delamination is found in *Polyxenia leucostyla* (Atlas, Plate VIII.). Unipolar immigration is illustrated by Fig. 4. It is the rule with metagenetic Hydromedusæ. The immigration continues until the central cavity is filled with a solid endoderm, which afterwards is hollowed out (Atlas, Plates II., III., IV.). Invagination has hitherto only been found in the Acraspeda (Nausithoe, Pelagia, Plate X., Atlas).—*H. V. W.*

cism of this hypothesis, which can lead us nowhere, and which must therefore be rejected.

The Gastræa theory, as is well known, has rendered great service in reducing the different phenomena of development to a primary invagination; it very often simplifies the complicated appearances sometimes seen in the formation of the endoderm, for instance, in the Vertebrates. But it is when the theory is called upon to explain delamination that it finds itself in the midst of difficulties of which Haeckel was aware when he first formulated his views on this subject. "The greatest cause for doubt," said he in his monograph on the "Calcareous Sponges" (vol. i. p. 467), "seems to lie in the fact that the gastrula may come from the morula by two quite different roads. In the one case it arises by a central hollowing out of the morula, the gastric cavity thus formed breaking through to the exterior. In the other case a blastosphere is formed, a hollow sphere whose wall consists of a single layer of cells; and the gastrula results from a pushing in of one part of this wall, in other words, from an invagination." Haeckel, however, thinks it possible to overcome this difficulty by assuming a "secondary falsification of the ontogeny." In his principal paper (17) he often repeats the assertion that delamination, in case it really occurs in the animal kingdom, is a cœnogenetic process, "which has secondarily arisen from the palingenetic process of invagination." As to the way in which such a falsification came about there is no explanation offered. This is the more to be regretted, as Haeckel himself felt the difficulty his theory encountered in this matter. Haeckel and his school, the Hertwig brothers in particular, long disputed the existence of delamination, but must surely admit it now, since a member of this very school, O. Hamann (26), has lately observed the process of delamination in the Hydroids (after it had been described by several previous investigators, among whom were Allman, F. E. Schulze, and myself). Hamann, however, will recognize no difficulty in this fact, and simply declares the delaminate planula to be a gastrula which has arisen by cœnogeny from an invaginate gastrula. "Delamination," states Hamann (l. c., p. 504), "is in all cases to be derived from invagination." "In view of the elsewhere universal presence of a gastrula," says he, farther on, "the doctrine, according to which a planula is but a transformed gastrula, will remain current." And yet again,

"We are justified in speaking of a form as a gastrula as soon as it can be made probable that the absence of both structures (blastosphere and gastric cavity) is of secondary origin. What we call a planula is, therefore, a gastrula formed by delamination." These assertions are made without adducing any grounds for their probability, and without making it in the least degree conceivable how invagination can be abbreviated into delamination, or what cœnogeny could effect for the origin of the latter. When one considers, moreover, that invagination is concentrated at one end of the embryo, and in the Medusæ is confined to a relatively small area of the blastoderm, while primary delamination or multipolar invagination takes place at the most various points of the embryo, it is evident that a reduction of the two latter methods to the former would meet with invincible difficulties. It is easy to understand how an invagination, originally confined to a small area, may gradually extend until, as is seen in various animals, it involves half the blastoderm. Further, one can see how a continuous layer of cells, destined to form the endoderm, may be changed into a cellular mass which is gradually enclosed by the growth of the ectoderm. But where the origin of the endoderm is an interrupted one,—that is, where the endoderm cells do not lie all together, but alternate with ectoderm cells (compare the development of Æginopsis), or where the endoderm appears as the central segments of the blastoderm cells,—it is impossible to refer the process to an abbreviated invagination. Multipolar immigration, to be sure, can be forcibly reduced to a number of invaginations, on which view each primitive gastric cavity would be represented by a single cell! It only needs to formulate such a hypothesis to demonstrate how utterly untenable it is; but, aside from this consideration, one would gain very little by accepting it, for primary delamination would still remain totally unexplained. It is between unipolar immigration and invagination that a relationship can fairly be assumed to exist, as has been maintained by Claus and others. It is impossible for me, however, without a previous discussion of other questions, to decide which form must be regarded as the more primitive.

Although its inability to explain the multipolar formation of endoderm is the weightiest objection to the Gastræa theory, it is by no means the only one. The theory was formulated at a time when the occurrence of intracellular digestion among the

lower Metazoa was not known, when in fact digestion in all cases (Metazoa) was believed to be enzymatic: naturally it is now unable to answer the questions suggested by our advanced physiological knowledge. The Gastræa theory would compel us to believe that a deep gap intervened between the one-layered blastosphere and the double-walled gastrula with its digestive cavity. This very awkward gap is, however, easily filled as soon as we abandon the Gastræa theory and seek to explain the origin of the endoderm in another manner. I need not dwell here upon the difficulties encountered by supposing all the known gastrula forms to be homologous. Such matters are not directly connected with our discussion of the primitive condition of the endoderm, and besides I shall have something to say on this point in another place.

The Planula theory of Ray Lankester (27) is based on the development of the Geryonidæ, and considers the method of forming the endoderm here employed, by constricting off the inner ends of the blastosphere cells, as the primitive type. Lankester endeavors to derive invagination from a primary delamination, such as occurs in Geryonia. But even were we satisfied with this derivation, there would still remain unexplained the cases where there is no actual delamination, but where the endoderm is formed of cells which migrate from various points of the surface into the interior of the embryo. The significance of this latter origin receives additional strength from unipolar immigration, the endoderm cells in both cases being blastoderm cells, which have arisen by longitudinal division from previous blastoderm cells. Moreover, the same objection must be raised to the Planula theory as to the Gastræa theory, namely, it rests on the assumption that digestion in the lower animals is enzymatic, and herein contradicts our actual physiological knowledge. Lankester believes that the formation of a cavity into which a digestive secretion was poured preceded the formation of the endoderm. In other words, the inner segments of the blastoderm cells functioned as digestive elements while the polyplast (blastula) was still one-layered. All these assumptions become quite inadmissible when once we learn that intracellular digestion persists in many of the lower Metazoa, and is even found in some Molluscs (Phylliroë).

While the Gastræa and Planula theories start with a blasto-

sphere composed of similar cells, Balfour (28, 29) adopts the amphiblastula as the transitional form between the Protozoa and Metazoa. I will therefore speak of his view as the Amphiblastula theory. Since it must be looked on as a modification of the Gastræa theory, it is open to the same objections as the latter. It is quite unable to explain the phenomena which occur when the endoderm does not arise as a single continuous structure, but as cells separated from one another by intervening ectoderm cells (the case of multipolar immigration especially). As regards the application of Balfour's theory to the Sponges, its untenability is shown by the fact that in many Sponges (especially Calcispongiæ and Halisarcinæ) the endoderm is a nutritive layer. This fact, already emphasized by early investigators and more than once by myself, has lately been confirmed by K. Heider (30) on *Oscarella lobularis.* The objection here raised, moreover, upsets the arguments which Balfour used to prove the isolated position of the Sponges among Metazoa.

Akin to the Amphiblastula theory is the Placula theory of Bütschli (22), not only because the latter author also believes in the separate descent of the Sponges, but because the placula in many respects may be considered as a flattened-out amphiblastula. Bütschli appreciates the weak points of other theories which deal with the genealogy of the germinal layers, and attempts in a purely diagrammatic way to construct the connection between invagination and delamination. He deduces both methods of forming the endoderm from the modification of a primary placula form. Abandoning the starting-point of other views,—the spherical colony of Flagellata,—our author adopts as his primitive form a Gonium-like one-layered plate, which for convenience I shall style proplacula. " It therefore seems fair to assume that the two layers first arose in a protozoan colony, the cells of which were arranged in one plane so as to form a one-layered plate. All the cells then divided parallel to the surface, and there thus arose a two-layered plate, the layers being probably as yet undifferentiated. To this stage of a two-layered plate we will give the name of placula." Such a placula, by assuming a sac-like form, became changed into a gastrula. In other cases the proplacula, in consequence of a secondarily retarded cell-division, gave rise to a delaminate blastosphere. As a result of these assumptions there would exist a radical difference in blasto-

spheres, which in some cases would represent swollen-up placulæ, in others proplaculæ that have become spherical. In the development of existing animals the placula, according to Bütschli, appears as the flattened blastosphere stage found in Cucullanus (Bütschli), Rhabdonema (Götte), Lumbricus, Chiton (Kowalevsky), Phoronis, and *Ascidia mentula.* Among adult animals it is represented by *Trichoplax adhærens* F. E. Sch. But Bütschli does not perceive that the flattened blastospheres of the Metazoa just mentioned agree with his placula in external form alone, and not in any essential or morphological respect. The fundamental difference between the two lies in the fact that the two layers of the former have not been acquired by cell-division parallel to the surface, which is the essence of the placula. In Phoronis, Ascidia, and, generally speaking, in the other animals cited above, the placula-like stage is attained by the flattening of a previously more or less spherical blastosphere, and not conversely as the theory requires. According to the theory the delamination of the Geryonidæ, accomplished by a transverse division of the blastoderm cells, is a process similar to the formation of a placula or amphiblastula, such as is supposed to occur in other animals. If this be true, we should find in the formation of this so-called placula a transverse division of the blastomeres. But this is not the case. The endoderm cells of the flattened blastospheres are not split off from the ectoderm cells immediately above them, but arise by the longitudinal division of parent cells. We are thus forced to the conclusion that a placula stage does not appear in the development of existing animals endowed with a regular segmentation. There is, however, a degree of similarity between the placula and a certain stage in the development of Ctenophores, where the endoderm has the form of a plate, and is covered by an interrupted layer of ectoderm. But this stage will scarcely be looked on by any one as embodying a primitive condition, and cannot, therefore, afford any basis for a morphological generalization.

If, going farther back in the development, we regard the eight-celled embryo formed by the transverse division of the first four blastomeres as a short-lived placula, we thereby gain nothing; for we must bear in mind that the eight-celled stage of the delaminating Geryonidæ is in all respects like the same stage of the invaginating Acraspeda, and must therefore be regarded as

homologous with it. If therefore the latter represents a placula, so must the former. But in this case the later delamination of the Geryonidæ, by means of transverse division of the blastosphere cells, could no longer be explained as the expression of a placula stage, because this stage would already have been passed.

Suppose, however, the assumption be correct that a placula stage occurs in the Metazoa with an invaginate gastrula. Then, since the placula theory can only explain the formation of endoderm, which takes place by means of a transverse division of the cells of a proplacula, all those cases would remain inexplicable where—the cell-division being exclusively longitudinal—the endoderm is formed by multipolar or local immigration.

According to Bütschli's theory, the blastosphere in animals that suffer delamination should be formed, as in Volvox, from a plate-like proplacula stage. He thinks, indeed (p. 423), the statements of Fol justify him in assuming the occurrence of such a stage in *Geryonia proboscidalis*. But the assumption is unwarranted, for the sixteen-celled embryo of the Geryonidæ is in itself a typical blastula, produced from an eight-celled stage precisely as in Medusæ which form their endoderm by a totally different method. The eight-celled embryo has likewise been produced by just such an equatorial division as occurs in other Medusæ and in most Metazoa with an equal segmentation. Among the latter *Sycandra raphanus*, according to F. E. Schulze's account, most nearly resembles Volvox as regards the stages preceding the blastosphere. In this sponge is found a plate-like eight-celled stage, which, however, can be of no value to the placula theory, since later on in the development there occurs an invaginate gastrula.

The morphology of the interesting *Trichoplax adhærens* F. E. Sch. (32) and its relations to the placula cannot be seriously discussed at the present time, since it is impossible to decide, with even a show of truth, what significance must be attached to the several layers of this animal. From the histological difference between the epithelial coverings of the two surfaces of the body, we cannot infer that different germinal layers were involved in the formation of these coverings, any more than in the Sponges where the same layer, the endoderm, appears in the chambers as flagellate epithelium and in the central cavity as flat epithelium

(for example, in *Oscarula lobularis*, according to K. Heider). The difficulties presented by Trichoplax are heightened not only by our ignorance of the development, but by our lack of any facts from which to determine the physiological functions of the several layers of the body. Thanks to the kindness of Professors F. E. Schulze and Claus, I was enabled in 1883 to study Trichoplax both at Graz and Vienna, and to fully confirm the histological discoveries of the former investigator. My experiments on the manner in which the animal fed gave purely negative results, for it would take no solid food at all, thereby lending countenance to the view that Trichoplax depends on fluid nourishment alone.

Bütschli thinks the Placula theory is of more value from a physiological point of view than the other theories criticised by him. "Finally, it seems to me very important," says Bütschli (l. c., p. 416), "that the changes undergone by the assumed forms are easily comprehended, that they take place gradually, not by jumps, and are actually advantageous." "Especially in this latter respect," adds Bütschli, "is the new view about to be developed superior to its predecessors." When, however, it comes to explaining physiologically the origin of the placula, no satisfactory reasons are given why it should arise. "I regret that I am unable to adduce," Bütschli confesses himself (p. 419), "any plausible advantages to be gained by the plate on its becoming two-layered."

(To be concluded.)

THE ORIGIN OF A SMALL RACE OF TURKEYS.

BY JOHN DEAN CATON, LL.D.

THE effect upon the progeny of animals of inbreeding, or where the parents are nearly related, is a subject well worthy the attention of naturalists, though I am not aware that it has been the subject of careful study, especially among the lower forms of animal life.

With man it has undoubtedly received much attention, but even here it has been rather of a desultory character than that careful and systematic attention which its practical importance